JUNE 1998

Full marks can be obtained for complete answers to FIVE questions.
Only the best FIVE answers will be counted.

1. The Hassell model for a single species with population $N_{t}$ at time $t$ is

$$
N_{t+1}=\left\{R /\left(1+a N_{t}\right)^{b}\right\} N_{t},
$$

where $R, a$ and $b$ are positive constants. Explain quite briefly why this is a useful model in population ecology.
Find the non-zero equilibrium population in the Hassell model and determine an inequality involving $R$ and $b$ which is satisified when this equilibrium state is stable. In the case $R=125, b=3$ and $a=1$ :
(i) Verify that the above equilibrium is not stable.
(ii) Determine $N_{t+2}$ in terms of $N_{t}$.
(iii) Show that there is a cycle of period 2 in which the population alternates between the two roots of the equation

$$
N^{2}-18 N+6=0 .
$$

2. The Richards growth law takes the form

$$
d N / d t=r N\left(1-K^{-5} N^{5}\right),
$$

where $r$ and $K$ are positive constants.
(i) Find the non-zero equilibrium value of $N$ and determine whether or not this is locally stable.
(ii) Using the substitution $u=N^{-5}$, or otherwise, integrate the above equation given that $N$ has an initial value $N_{0}<K$. Determine the behaviour of the solution for large times.
(iii) Construct a difference equation - with time interval $\tau$ - analogous to the above differential equation. Find the non-zero equilibrium value of $N$. Investigate the local stability of this equilibrium. Very briefly compare your results with those of (i).
3. State carefully a theorem involving a Liapunov function $V$ which guarantees the asymptotic stability of an equilibrium point in population dynamics.
A 'toy' model for a predator-prey system has equations

$$
\begin{gathered}
d x / d t=a y+x\left(x^{2}+y^{2}-2\right), \\
d y / d t=-a x+y\left(x^{2}+y^{2}-2\right),
\end{gathered}
$$

where $x(t)$ and $y(t)$ denote departures from equilibrium and $a$ is a positive constant. Use the above theorem with $V=x^{2}+y^{2}$ to show that the equilibrium state is asymptotically stable.

Obtain the exact general solution of the above equations using polar coordinates $r$ and $\theta$. Hence verify the result deduced from the Liapunov theorem.

Given the initial value of $r$ is $r_{0}$, sketch trajectories in the $X-Y$ phase plane describing the behaviour of the system for $r_{0}<\sqrt{2}, r_{0}=\sqrt{2}$ and $r_{0}>\sqrt{2}$. Explain briefly how this behaviour is affected by varying the parameter $a$ in the above equations.
4. An $m$-species ecosystem evolves according to the difference equations

$$
x_{i}(t+\tau)-x_{i}(t)=\tau F_{i}\left(x_{1}(t), \ldots, x_{m}(t)\right), i=1,2, \ldots, m
$$

in which $x_{i}(t)$ is the population density of the $i$ th species at time $t$ and $\tau(>0)$ is the time interval between breeding seasons for all species.

Derive an approximation to these equations, involving the community matrix, which is valid sufficiently close to an equilibrium point. On the assumption that there is a basis of eigenvectors of the community matrix, find the general solution to these approximate equations.

A particular 3- species system has growth equations

$$
\begin{aligned}
x_{1}(t+\tau)-x_{1}(t) & =\tau x_{1}\left(4-x_{1}-3 x_{2}+3 x_{3}\right) \\
x_{2}(t+\tau)-x_{2}(t) & =\tau x_{2}\left(4+3 x_{1}-4 x_{2}\right) \\
x_{3}(t+\tau)-x_{3}(t) & =\tau x_{3}\left(4 \quad+3 x_{2}-4 x_{3}\right) .
\end{aligned}
$$

Find values of $x_{1}, x_{2}, x_{3}$ for which the system possesses a point equilibrium state $(Q)$ with all species present.

Determine the community matrix $(A)$ associated with the state $Q$ and find the eigenvalues of $A$.

Hence find the range of values of $\tau$ for which the state $Q$ is locally stable.
5. The growth equations for an ecosystem involving $m$ species $X_{1}, \ldots, X_{m}$ which compete for a resource $R$ in a habitat $D$ are given by

$$
d x_{i} / d t=x_{i}\left(k_{i}-\sum_{j=1}^{m} \alpha_{i j} x_{j}\right), i=1,2, \ldots, m,
$$

in which $x_{i}(t)$ is the population density of species $X_{i}$ at time $t$ and the $k_{i}, \alpha_{i j}$ are positive constants. State the biological significance of the constants $\alpha_{i j}$ for the separate cases $i=j$ and $i \neq j$.

The utilisation of $R$ by $X_{i}$ can be represented by the function

$$
f_{i}=\frac{C}{\sqrt{\omega}} \exp \left[\frac{-(\theta-i d)^{2}}{2 \omega^{2}}\right]
$$

for $i=1,2, \ldots, m$, where $C, \omega$ and $d$ are positive constants and $\theta$ describes the variation of $R$ in $D$. Explain briefly why it is reasonable to set

$$
\alpha_{i j}=\int_{-\infty}^{\infty} f_{i}(\theta) f_{j}(\theta) d \theta
$$

Show that, for a suitable choice of $C$,

$$
\alpha_{i j}=\alpha^{(i-j)^{2}} \text { with } \alpha=\exp \left(-d^{2} / 4 \omega^{2}\right) .
$$

Given that the system possesses an equilibrium state $Q$ with $x_{i}=N(\neq 0)$ for all $i$, find the community matrix $A$ associated with $Q$ using cyclic boundary conditions.
Determine the eigenvalues of $A$ in the case $m=3$ and hence discover whether in this case the state $Q$ is locally stable.
6. Write down, in terms of the eigenvalues of the community matrix, the local stability conditions used in population dynamics for, first, a continuous time model and, second, the corresponding, analogous discrete time model.
Let

$$
\begin{aligned}
& f_{1}\left(N_{1}, N_{2}\right)=7 N_{1}\left[1-K^{-1} N_{1}-\frac{21}{25}\left(N_{1}+\frac{4}{25} K\right)^{-1} N_{2}\right], \\
& f_{2}\left(N_{1}, N_{2}\right)=N_{2}\left[1-N_{1}^{-1} N_{2}\right],
\end{aligned}
$$

where $K$ is a positive constant.
Locate the coexistence equilibrium and determine its local stability properties in the case where

$$
\begin{aligned}
& d N_{1} / d t=f_{1}\left(N_{1}, N_{2}\right), \\
& d N_{2} / d t=f_{2}\left(N_{1}, N_{2}\right) .
\end{aligned}
$$

Determine the equivalent equilibrium and stability properties in the case where

$$
\begin{aligned}
\tau^{-1}\left[N_{1}(t+\tau)-N_{1}(t)\right] & =f_{1}\left(N_{1}, N_{2}\right), \\
\tau^{-1}\left[N_{2}(t+\tau)-N_{2}(t)\right] & =f_{2}\left(N_{1}, N_{2}\right),
\end{aligned}
$$

where the notation is standard.
Briefly compare your continuous-time and discrete-time results.
7. An ecosystem involves four species with respective population densities $x_{1}(t), x_{2}(t)$, $x_{3}(t)$, and $x_{4}(t)$ at time $t$. The evolution of the system is described by a continuous-time model with growth equations

$$
\begin{aligned}
& d x_{1} / d t=x_{1}\left(-4 \quad+x_{2}+2 x_{3}+x_{4}\right) \\
& d x_{2} / d t=x_{2}\left(-2-x_{1} \quad+x_{3}+2 x_{4}\right) \\
& d x_{3} / d t=x_{3}\left(2-2 x_{1}-x_{2}+x_{4}\right) \\
& d x_{4} / d t=x_{4}\left(4-x_{1}-2 x_{2}-x_{3}\right)
\end{aligned}
$$

Explain briefly the kind of interaction which occurs between each pair of species.
Verify that the system possesses an equilibrium state $(Q)$ with $x_{1}=x_{2}=x_{3}=x_{4}=1$. Find the community matrix $A$ associated with $Q$. Either by proving a general result about matrices with the same structure as $A$ or otherwise show that the eigenvalues of $A$ are purely imaginary. Hence describe briefly the behaviour of the system close to $Q$. The quantity $\psi$ is defined by

$$
y=x_{1}+x_{2}+x_{3}+x_{4}-\ln \left(x_{1} x_{2} x_{3} x_{4}\right)
$$

Show that, as the system evolves, $\psi$ remains constant.
State briefly how this is related to the nature of the stability of the equilibrium state $Q$.

